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AUGUST WEISMANN.

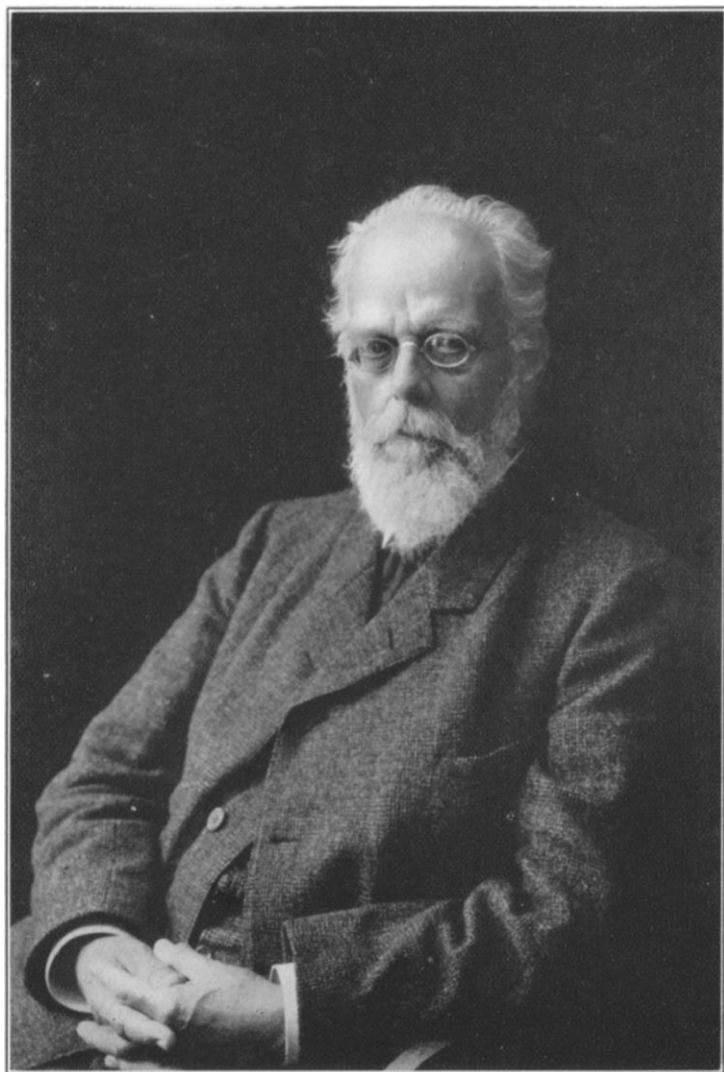
PLATE A.

(Read January 1, 1915.)

August Weismann, a foreign member of this Society, was born at Frankfort on the Main, January 17, 1834, and died at Freiburg in Breisgau, November 6, 1914. He early showed the traits of a naturalist and in one of his books speaks of the excitement he felt as a boy in catching butterflies. He attended the University of Göttingen, where he studied chemistry and medicine, coming especially under the instruction of the distinguished anatomist Henle, and receiving the degree of M.D. in 1856. After spending three years at Rostock as an assistant he began the practice of medicine at Frankfort and during this time he visited Vienna in 1858, Italy in 1859 and Paris in 1860. From 1861 to 1862 he was private physician to Archduke Stephan of Austria at Schamburg Palace. He then studied zoölogy at Giessen under the renowned zoölogist Leuckart and became *privat-docent* in zoölogy at the University of Freiburg in 1863, where he spent the remainder of his life. In 1866 he was appointed *professor extraordinarius* and a few years later became *professor ordinarius*, which position he continued to hold until a few years before his death, when he was made *professor emeritus*.

In person he was a man of striking appearance, being about six feet tall and well proportioned and having a fine head and face and an earnest but kind expression of the eyes. From 1864 to 1874 and again from 1884 on he suffered from an eye trouble which interfered greatly with his microscopical work and turned his attention to theoretical questions. One of his former students and assistants, Professor Alexander Petrunkevitch,¹ to whom I am indebted for much valuable information concerning his personality,

¹ I am also indebted to Prof. H. H. Wilder, of Smith College, and to Prof. J. S. Kingsley, of the University of Illinois, for information regarding the family life and personality of Weismann.



AUGUST WEISMANN.

BORN JANUARY 17, 1834. DIED NOVEMBER 6, 1914.

says that although he was usually quiet in manner he invariably became nervous and unhappy in the presence of moving objects, which painfully affected his eyes.

A short autobiography published in *Lamp* in 1903 gives a glimpse of his family life:

"During the ten years (1864-1874) of enforced inactivity and rest occurred my marriage to Fraulein Marie Gruber, who became the mother of my children and was my true companion for twenty years until her death. Of her now I think only with love and gratitude. She was the one who more than any one else helped me through the gloom of this period. She read much to me at this time, for she read aloud excellently, and she not only took an interest in my theoretical and experimental work but she also gave practical assistance in it."²

His great work on the "Natural History of the Daphnoidea" (1876-79) is dedicated to "My father-in-law, Adolph Gruber, in thankful memory of the beautiful hours of leisure spent on the shores of Bodensee." His colleague, the anatomist Wiedersheim, married another daughter of Gruber who was a Genoese banker. After the death of his first wife Weismann married again when about sixty years old, but not happily. One of his daughters married the zoölogist W. N. Parker, who translated into English his best known work "The Germ Plasm." A son was trained as a professional violinist.

Weismann, like so many other naturalists, was of an artistic disposition. He loved nature, art and music and he was an accomplished pianist. During the periods when he suffered much from his eye trouble he says that he "found solace in playing a good deal of music." He was an enthusiastic admirer of Beethoven but could not appreciate Wagner. His artistic temperament is further shown in many of his essays which for beauty of expression are rarely surpassed in scientific literature.

He was an excellent speaker, being simple and earnest in manner and never indulging in jokes. His lectures on evolution, which were delivered regularly for almost forty years, were famous and always attracted great audiences. As a teacher of advanced students he was stimulating and helpful, a kind critic and an attentive listener.

He took no active part in politics, but like many German pro-

² Quoted from Locy's "Biology and its Makers," p. 401.

fessors was a member of the "National Liberal" party. In philosophy he held tenaciously to a mechanistic conception of nature, but he believed that extreme mechanism was consistent with extreme teleology, indeed he held that "The most complete mechanism conceivable is likewise the most complete teleology conceivable. With this conception vanish all apprehensions that the new views of evolution would cause man to lose the best that he possesses—morality and purely human culture." In his philosophy as in his scientific controversies he was extremely tolerant. He was interested in the promotion of knowledge but was not aggressive nor offensive in manner.

Inasmuch as his life was so largely given to the extension and support of the Darwinian theory it is interesting to hear from himself how that theory first came to his attention. After remarking, "I never heard evolution referred to in my student days," he describes the influence on himself of Darwin's book in these words:

"I myself was at the time in the stage of metamorphosis from a physician to a zoölogist, and as far as philosophical views of nature were concerned I was a blank sheet of paper, a *tabula rasa*. I read the book ["Origin of Species"] first in 1861 at a single sitting (*sic*) and with ever growing enthusiasm. When I had finished I stood firm on the basis of the evolution theory, and I have never seen reason to forsake it."

With just pride he mentions the fact that he was one of the first scientific men in Germany to defend publicly Darwin's theory; Fritz Müller was the first to publish a work in favor of that theory ("Für Darwin," 1864), Haeckel was the second ("Generelle Morphologie," 1866) and Weismann was the third, his Inaugural Address at Freiburg on the "Justification of the Darwinian Theory" ("Über die Berechtigung der Darwin'schen Theorie") being published in 1868.

Thereafter his contributions to the Darwinian theory were numerous and important. They appeared from 1872 to 1902 as a series of books and contributions. Five of these earlier contributions were translated into English by R. Meldola and were published as two large volumes in 1882 with an introduction by Charles Darwin. Subsequent studies on evolution were so intimately associated with his theories of heredity that they can best be considered under that topic.

Weismann's contributions to biological theory were so extensive and important that they overshadow to a great extent his observational and experimental work, and yet the latter was by no means small or unimportant. Among these observational and experimental studies must be mentioned especially his extensive works on "The Development of Diptera (1865)," "Natural History of the Daphnoidea" (1876-79), "Origin of the Sex Cells of the Hydromedusæ (1883)," "Seasonal Dimorphism of Butterflies" (1875), "Origin of Markings of Caterpillars" (1876) and "Transformation of the Mexican Axolotl into Amblystoma."

Some of his earlier work was done without assistance, but in all of his later observational and experimental studies he had the assistance of his wife or other helpers. Much of his work was done in collaboration with some of his students or assistants. His method of work was to a large extent forced upon him by his eye affliction. After 1864 all reading had to be done for him, at first by his wife and after her death by a secretary. Experimental work was done under his supervision by his assistant and janitor. All microscopic work was done by his pupils, to whom he suggested topics and whose work he supervised daily. These theses were always in direct relation to his theories and to that phase of them which interested him most at the moment.

But valuable as much of his observational and experimental work was, there is no doubt that he will be remembered chiefly for his theories of heredity. His earliest writings on this subject date from the year 1883 and his latest were published but a few years before his death. His "Essays upon Heredity and Kindred Biological Topics" were translated into English and published in two volumes in 1889 and 1892. Probably his most important work on this subject is his book entitled "The Germ-Plasm, A Theory of Heredity" which was published in English in 1893. Subsequent works on heredity are "On Germinal Selection" (1896) and "Vorträge über Descendenztheorie" (1902). This last-named work, which was published in English under the title "The Evolution Theory" (1904), consists of a summary and an expansion of many of his previous writings on the subjects of evolution and heredity;

indeed as he says in the preface of this book, it is "a mirror of the course of my own intellectual evolution."

Without attempting to analyze these different books, which would require more time and space than is here available, we may proceed at once to a summary of his more important contributions to the theories of evolution and heredity.

All his theories, both of heredity and evolution, center in what he called the "germ-plasm," that particular part of the germ cells which serves to carry over from generation to generation the inheritance factors. This germ-plasm was held by Weismann to be absolutely *continuous* from the present generation back to the earliest generations of living things; it was absolutely *distinct* from the somatoplasm of the body and the latter could never become germ-plasm; it was almost perfectly *stable* undergoing practically no changes except such as came from the mixing of different kinds of germ-plasm (amphimixis) in sexual reproduction.

These views as to the nature of the germ-plasm underwent some modification as the result of criticism. Weismann was forced to admit that the distinctness and stability of the germ-plasm were not absolute, but in spite of all criticism he was able to maintain that the germ-plasm was relatively very distinct from other plasmas and very stable in organization and this is now admitted by all persons acquainted with the subject.

His views as to the separateness of somatoplasm and germ-plasm, of body cells and germ cells, and the mortality of the former and potential immortality of the latter, led him to regard organisms in which this distinction does not exist (many protozoa and proto-phyta) as potentially immortal. With a keenness of insight which was not appreciated at the time but which has been confirmed by recent work he reasoned that "conjugation like food and oxygen may be conditions of life but immortality does not rest on the magic of conjugation any more than on food or oxygen." Again he anticipated the most recent opinions when he held that death is not a necessary correlative of life, but rather the result of higher differentiation. In short, as Minot said, "Death is the price we pay for our differentiation." On the other hand, his attempt to

explain the origin of death as an adaptation due to selection was probably a mistaken one.

As to the location of the germ-plasm in the sex cells Weismann maintained that it was to be found in the chromatic substance of the nucleus. He held that the chromosomes ("idants") were composed of smaller units, the chromomeres ("ids"), and that the latter were composed of "determinants" or inheritance units, while the most elementary units of life he called "biophores." Both chromosomes and chromomeres are visible structures of the cell. Determinants and biophores are ultra-microscopic in size but recent work on heredity and development has shown that there is good evidence of the existence of such units. All recent work in genetics is based upon the hypothesis that there are units or factors or determiners in germ cells which condition the development of adult characters, and though there may be minor differences between these *determiners* of modern genetics and the *determinants* of Weismann no one can fail to note the genetic connection and the family resemblance between the two.

His prediction on purely *a priori* grounds that one of the maturation divisions in the formation of the egg and sperm should be a "reduction division" whereby the chromosomes of the sex cells should be reduced to half the number present in the somatic cells, whereas all other cell divisions should be "equation divisions" in which the chromosomes should divide equally, was almost as brilliant an example of scientific prophecy as was the prediction of the existence of the planet Neptune.

Similarly Weismann's assumption that the determinants are arranged in a linear series in the chromosomes finds strong support in the newest and most striking discoveries in this field, in which Morgan is able to locate at different points along the length of a chromosome the determiners of many developed characters.

Finally there is at present universal agreement to the declaration of Weismann that no purely epigenetic theory of heredity is possible, though for many years even this was hotly contested. When one recalls the storm of opposition which was called forth by his book on "The Germ-Plasm" the present acceptance, at least

in principle, of his major propositions cannot be viewed in any other light than as a triumph for his theory and a tribute to the insight, foresight and constructive ability of Weismann.

As a result of his theory of heredity Weismann was led to investigate the generally accepted doctrine of the inheritance of acquired characters. He carried on extensive experiments in order to learn whether mutilations of parents through many generations were ever inherited by offspring; he investigated many supposed cases of the inheritance of such characters, and as a result of this work he was led to deny altogether the possibility of the inheritance of acquired characters, and he challenged the world to furnish any satisfactory proof of such inheritance. This work of Weismann's called forth a tremendous amount of discussion and a relatively small amount of direct observation and experiment, and for several years it appeared as if no progress whatever was being made toward the solution of this great question, so full of importance, not merely for the biologist but also for the practical breeder and indeed for the human race. But gradually there has grown up a clearer understanding of the problem and of what is meant by "inherited" and "acquired" characters, and gradually this dead-lock of opinions is breaking up. Now we recognize that inherited characters are those whose distinctive or differential causes are in the germ cells, while acquired characters are those whose differential causes are environmental. No one today believes that the developed or somatic characters of an organism are transmitted to the next generation. Today the problem of the inheritance of acquired characters is merely this: Can changes in the environment change the constitution of the germ-plasm so as to produce changes in subsequent generations? No one now asks whether changes in developed characters may be transmitted to descendants, as was generally done before Weismann's work, for it is generally recognized that somatic characters whether inherited or acquired are not transmitted from generation to generation, the only thing which is transmitted being the germ-plasm. Weismann admitted in his later writings that the germ-plasm might be modified to a limited extent by certain environmental conditions, but he held that such

changes of the germ-plasm led to general and unpredictable changes in future generations which might be wholly different from those somatic changes in the parents which were directly produced by such environment. This view is now widely accepted.

Thus while Weismann's views on this subject underwent certain changes in the course of his long life, the opinions of his opponents have undergone so much greater and more important changes that it may be truly said that in the matter of the inheritance or non-inheritance of acquired characters the greater portion of the scientific world has come to Weismann's position.

Finally mention must be made of Weismann's theory of evolution which was a direct outgrowth of his theory of heredity. He maintained that evolution must depend upon an evolution of the germ-plasm and that this was brought about chiefly, if not entirely, by the mixture of different kinds of germ-plasms (amphimixis) in the union of the sex cells. There is no doubt that many variations are produced by amphimixis but in general these combinations of germ-plasms are not actual fusions; new combinations of inheritance units are produced but not new units, and usually these new combinations split up in subsequent generations according to Mendelian rules, so that such temporary combinations of different germ-plasms do not usually lead to permanent modification, or to evolution, of the germ-plasm. On the other hand it is probable that Weismann underestimated the possible influence of environment in producing changes in the germ-plasm and hence its influence on evolution; at least it does not seem possible at present to explain the origin of many inherited mutations except by the influence of changed environment upon the developing germ cells.

In his belief in Natural Selection Weismann out-Darwined Darwin or any of the Darwinians. Darwin dealt only with the survival of individuals or races in the struggle for existence and was always inclined to assign a good deal of weight to the influence of environment in producing new races. Weismann would not admit the existence of any other factor of evolution than selection and he extended this principle from individuals or persons ("personal selection") to organs and tissues ("histonal selection") and

even to germinal units such as determinants and biophores ("germinal selection"). By means of an assumed struggle for nutriment between different determinants he believed that the weaker ones would tend to grow still weaker and to disappear while the stronger ones would increase in strength until they reached such importance that they were checked, or increased, by personal selection. And by a similar struggle between different biophores he showed that the *quality* of a determinant would be changed. By means of this highly ingenious but purely formal and hypothetical system he was able to explain the degeneration and disappearance of useless parts of an organism and the concordant modification of many different parts in the course of evolution.

Of all his theories those which grew out of his belief in the "Omnipotence of Selection" have found least confirmation in subsequent work. The Mutation Theory of deVries has come in to modify in certain important respects the theory of Darwin, and the work of Johannsen, Jennings, Pearl and others has shown that even "personal selection" has little or no influence in *creating* new types. And yet we have not seen the end of the selection doctrine. The elimination of the unfit is still the only natural means of accounting for fitness in organisms and we may well ponder these words of Weismann in the preface of his last book:

"Although I may have erred in many single questions which the future will have to determine, in the foundation of my ideas I have certainly not erred. The selection principle controls in fact all categories of life units. It does not create the primary variations but it does determine the paths of development which these follow from beginning to end, and therewith all differentiations, all advances of organization and finally the general course of development of organisms on our earth, for everything in the living world rests on adaptation."

Clear thinking is necessary in the advance of science as well as fine technique and Weismann has demonstrated to a more or less scornful world the importance of brains as well as of hands and eyes in the discovery of truth. It does not fall to the lot of any man to make no mistakes, and in this respect Weismann was only human. But it has fallen to the lot of few men to do so much work of lasting value and to have so profound an influence on his

day and generation as was true of August Weismann. The spirit of his life and work may be summed up in the beautiful words with which he closes his essay on "Life and Death": "After all it is the quest after perfected truth, not its possession, that falls to our lot, that gladdens us, fills up the measure of our life, nay! hallows it."

EDWIN G. CONKLIN.

PRINCETON UNIVERSITY,
January, 1915.